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Neotropical Monogenoidea. 31. Ancyrocephalinae (Dactylogyridae) of Piranha and Their Relatives (Teleostei, Serrasalmidae) from Brazil: Species of *Notothecium* Boeger and Kritsky, 1988, and *Enallothecium* gen. n.

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ABSTRACT: Eight species (7 new) of *Notothecium* and 4 species (3 new) of *Enallothecium* (Dactylogyridae, Ancyrocephalinae) are described or reported from the gills of 11 species of Serrasalmidae from the Brazilian Amazon: *Notothecium circellum* sp. n., from *Serrasalmus gouldingi* and *Pristobrycon* sp.; *N. cyphophallum* sp. n., from *Pristobrycon eigenmanni, Pristobrycon* sp., *Serrasalmus compressus, S. elongatus, S. gouldingi, S. rhombeus, Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. (2*n* = 58); *N. deleastoideum* sp. n., from *Serrasalmus* sp. (2*n* = 58); *N. deleastum* sp. n., from *Serrasalmus elongatus, S. gouldingi, S. rhombeus,* and *Serrasalmus* sp. (2*n* = 58); *N. mizellei* Boeger and Kritsky, 1988, from *Pygocentrus nattereri*; *N. modestum* sp. n., from *Serrasalmus spilopleura*; *N. phyleticum* sp. n., from *Serrasalmus rhombeus*; *N. reduvium* sp. n., from *Serrasalmus* sp. (2*n* = 58) and *Serrasalmus* sp. (2 of Jégu); *Enallothecium aegidatum* (Boeger and Kritsky, 1988) comb. n. (syn. *Notothecium aegidatum* Boeger and Kritsky, 1988), from *Pristobrycon* sp., *Pygocentrus nattereri, Serrasalmus compressus, S. elongatus, S. gouldingi, S. rhombeus, S. spilopleura, Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. (2*n* = 58); *E. cornutum* sp. n., from *Pristobrycon eigenmanni, Pristobrycon* sp., *Serrasalmus compressus, S. gouldingi, S. rhombeus, Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. (2*n* = 58); *E. umbelliferum* sp. n., from *Serrasalmus compressus, S. rhombeus,* and *Serrasalmus* sp. (2 of Jégu); and *E. variabilum* sp. n., from *Pristobrycon striolatus. Enallothecium* gen. n. is proposed and is characterized by dactylogyrids with overlapping gonads, a C-shaped seminal vesicle, an oblique opening of the male copulatory organ, a flap-like thumb and an umbell of the accessory piece, and a vagina looping the left intestinal cecum and opening at the tip of a small papilla on the sinistrodorsal surface of the trunk. *Notothecium aegidatum* Boeger and Kritsky, 1988, is transfered to *Enallothecium* as the type species of the genus.

KEY WORDS: Monogenoidea, Dactylogyridae, Ancyrocephalinae, *Enallothecium* gen. n., *Notothecium, Enallothecium aegidatum* comb. n., *Enallothecium cornutum* sp. n., *Enallothecium umbelliferum* sp. n., *Enallothecium variabilum* sp. n., *Notothecium circellum* sp. n., *Notothecium cyphophallum* sp. n., *Notothecium deleastoideum* sp. n., *Notothecium deleastum* sp. n., *Notothecium mizellei, Notothecium modestum* sp. n., *Notothecium phyleticum* sp. n., *Notothecium reduvium* sp. n., Serrasalmidae, *Pristobrycon eigenmanni, Pristobrycon striolatus, Pristobrycon* sp., *Pygocentrus nattereri, Serrasalmus compressus, Serrasalmus elongatus, Serrasalmus gouldingi, Serrasalmus rhombeus, Serrasalmus spilopleura, Serrasalmus* sp., Amazon Basin, Brazil.

This paper is the last of 4 contributions dealing with Ancyrocephalinae from the gills of Serrasalmidae from the Brazilian Amazon (see Kritsky et al., 1996, 1997a, b) and includes the report or description of 8 species (7 new) of *Notothecium* Boeger and Kritsky, 1988, and 4 species (3 new) of *Enallothecium* gen. n. *Notothecium aegidatum* Boeger and Kritsky, 1988, is transfered to *Enallothecium* as its type species.

Methods of host (*Pristobrycon eigenmanni* (Norman); *P. striolatus* (Steindachner); *Pristobrycon* sp.; *Pygocentrus nattereri* (Kner); *Serrasalmus compressus* Jégu, Leão, and dos Santos; *S. elongatus* Kner; *S. gouldingi* Fink and Machado-Allison; *S. rhombeus* (Linnaeus); *S. spilopleura* Kner; *Serrasalmus* sp. (2*n* = 58); and *Serrasalmus* sp. (2 of Jégu)) and parasite collection, and preparation of helminths for study, measurement, and illustration are those of Kritsky et al. (1986, 1996). Measurements, all in μm, represent straight-line distances between extreme points and are expressed as a mean followed by the range and number of specimens measured in parentheses; body length includes

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that of the haptor; length of the accessory piece is that of the distal rod. Measurements of internal organs (gonads and pharynx), the body, and haptoral bars were obtained from stained unflattened specimens; those of the anchors, hooks, and copulatory complex were from unstained specimens mounted in Gray and Wess' medium. Numbering (distribution) of hook pairs follows that recommended by Mizelle (1936; see Mizelle and Price, 1963). Type and voucher specimens are deposited in the helminth collections of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); the United States National Parasite Collection, Beltsville, Maryland (USNPC); and the University of Nebraska State Museum, Lincoln, Nebraska (HWML), as indicated in the respective descriptions or accounts. For comparative purposes, 2 paratypes (HWML 23363) and 3 vouchers (HWML 23397) of *Notothecium mizellei* were examined.

Presumed undescribed hosts have been provisionally identified by Jégu as *Pristobrycon* sp., *Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. ($2n = 58$). Representative specimens, cataloged as *Pristobrycon* sp., *Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. ($2n = 58$) from respective localities, are in the ichthyology collection of INPA.

Taxonomic Account

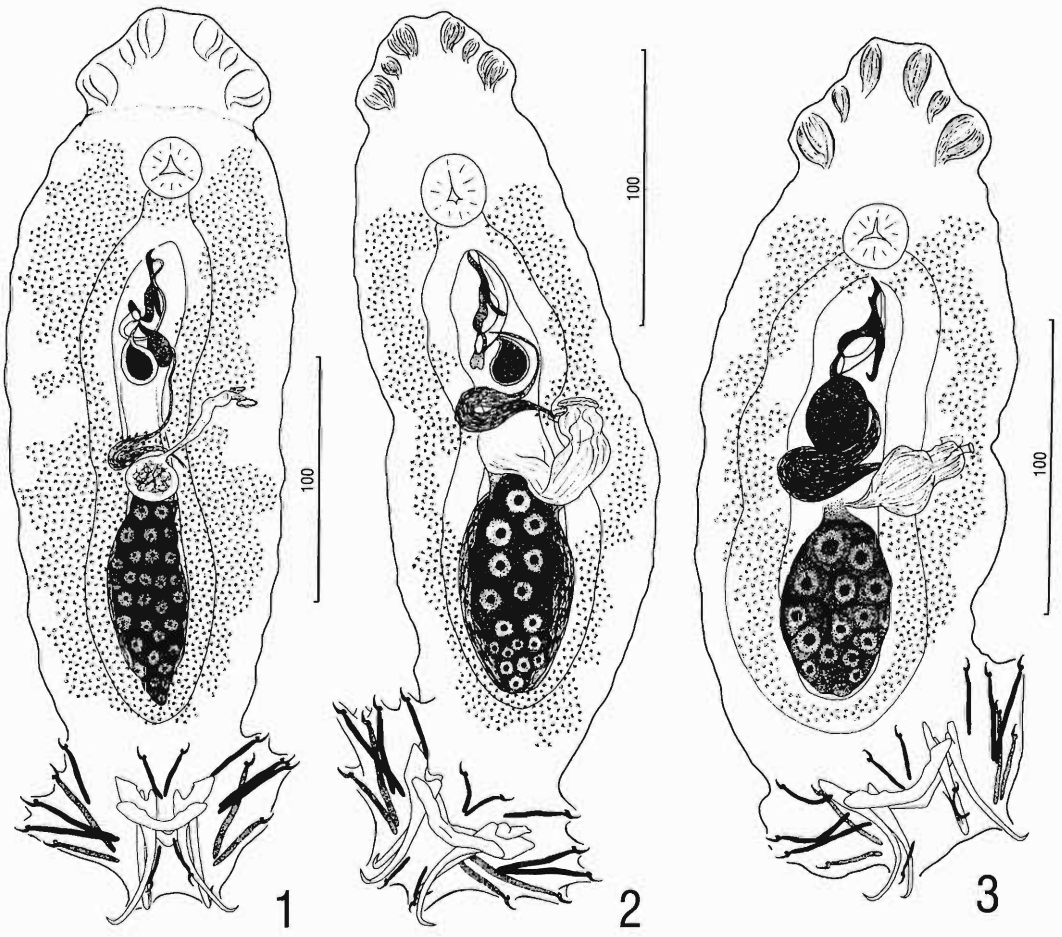
Class Monogenoidea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Dactylogyridae Bychowsky, 1933
Notothecium Boeger and Kritsky, 1988

EMENDED DIAGNOSIS: Body somewhat flattened dorsoventrally, comprising cephalic region, trunk, peduncle, haptor. Tegument thin, smooth or with scaled annulations. Two terminal, 2 bilateral cephalic lobes; head organs present; cephalic glands unicellular, lateral, or posterolateral to pharynx. Eyes absent; accessory granules (when present) elongate ovate. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; intestinal ceca 2, confluent posterior to gonads, lacking diverticula. Gonads intercecal, overlapping; testis dorsal to germarium. Vas deferens looping left intestinal cecum; seminal vesicle a C-shaped dilated loop of vas deferens extending into right half of trunk; 1 or 2 prostatic reservoirs. Copulatory complex comprising articulated copulatory organ, accessory piece; copulatory organ usually arcuate with 1 or 2 rami; accessory piece comprising distal rod with thumb, proximal articulation process. Seminal receptacle absent (functionally replaced by vaginal sperm storage) or present. Vagina looping left intestinal cecum, dilated, nonsclerotized, with subterminal ventral pouch; primary vaginal aperture simple, sinistrodorsal; ventral pouch may open as secondary vaginal aperture on sinistroventral body surface; vaginal vestibule absent. Genital pore midventral near level of intestinal bifurcation. Vitellaria coextensive with intestine. Haptor subhexagonal, with dorsal and ventral anchor/bar complexes, 7 pairs of hooks with ancyrocephaline distribution. Hooks similar; each with delicate point, truncate protruding thumb, expanded shank comprising two subunits; proximal subunit variable in length between hook pairs. FH loop extending to union of shank subunits. Ventral bar lacking anteromedial projection. Parasites of gills of serrasalmid fishes.

TYPE SPECIES: *Notothecium mizellei* Boeger and Kritsky, 1988, from *Pygocentrus nattereri.*

OTHER SPECIES: *Notothecium circellum* sp. n. from *Serrasalmus gouldingi* (type host) and *Pristobrycon* sp.; *N. cyphophallum* sp. n. from *P. eigenmanni, Pristobrycon* sp., *S. compressus, S. elongatus, S. gouldingi, S. rhombeus* (type host), *Serrasalmus* sp. ($2n = 58$), and *Serrasalmus* sp. (2 of Jégu); *N. deleastoideum* sp. n. from *Serrasalmus* sp. ($2n = 58$); *N. deleastum* sp. n. from *S. elongatus, S. gouldingi, S. rhombeus* (type host), and *Serrasalmus* sp. ($2n = 58$); *N. modestum* sp. n. from *S. spilopleura; N. phyleticum* sp. n. from *S. rhombeus; N. reduvium* sp. n. from *Serrasalmus* sp. ($2n = 58$) (type host), and *Serrasalmus* sp. (2 of Jégu).

REMARKS: Boeger and Kritsky (1988) proposed *Notothecium* for their new species, *N. mizellei* and *N. aegidatum.* The genus was characterized by species with a single vagina looping the left intestinal cecum, a sinistrodorsal vaginal aperture, overlapping gonads, and a C-shaped seminal vesicle. Our discovery of additional species of this group supports removal of *N. aegidatum* from *Notothecium* and proposal of *Enallothecium* gen. n. *Notothecium* is now characterized by an additional character, presence of a subterminal vaginal pouch that may open on the sinistroventral surface of the body (i.e., some species of *Notothecium* may have both sinistrodorsal and sinistroventral vaginal apertures) (see Figs. 1–3). It is separated from *Enallothecium* by lack-



Figures 1–3. Whole mount illustrations of *Notothecium* spp. (composite, ventral views). 1. *Notothecium circellum* sp. n. (from *Serrasalmus gouldingi*. 2. *Notothecium cyphophallum* sp. n. (from *Serrasalmus rhombeus*). 3. *Notothecium deleastoideum* sp. n. All drawings are to respective 100-μm scales.

ing an umbell in the accessory piece, a papillum at the vaginal aperture, a diagonal opening of the tip of the primary ramus of the copulatory organ, and an accessory flap extending over the thumb of the distal rod of the accessory piece (all apparent synapomorphic features of *Enallothecium*). *Notothecium* may be confused with *Calpidothecium,* but species in the latter genus lack the vaginal loop of the left intestinal cecum (vagina opening on the left lateral margin of the trunk in *Calpidothecium* species).

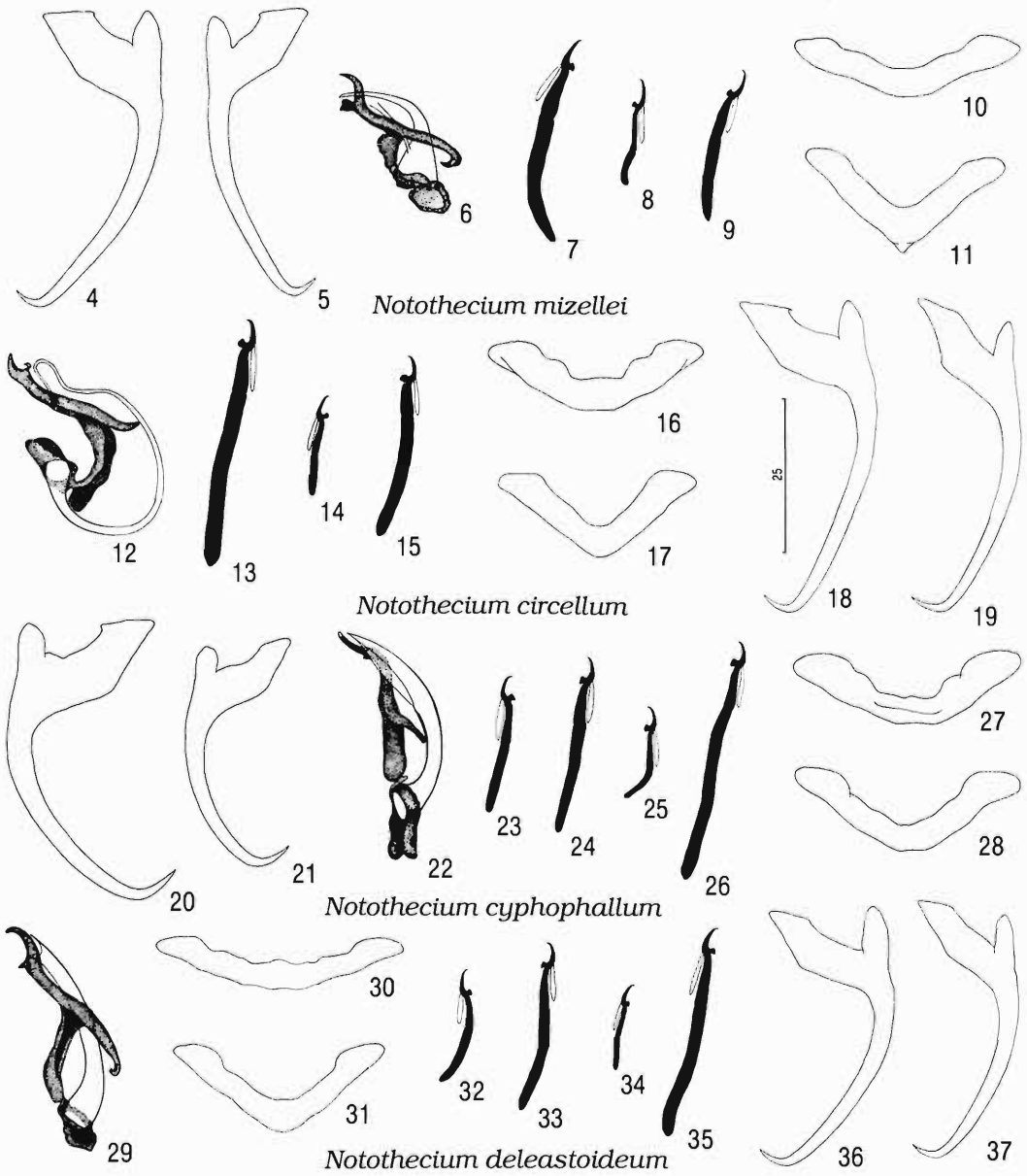
Notothecium mizellei Boeger and Kritsky, 1988
(Figs. 4–11)

RECORDS: *Pygocentrus nattereri:* Rio Uatumã Lago Tapaná near Santana, Amazonas (3 November 1989); Furo do Catalão, Manaus, Amazonas (27 November 1984).

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas (type locality); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas; Rio Pacaás-Novos, Guajará-Mirim, Rondônia; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia; Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

SPECIMENS STUDIED: Two paratypes, HWML 23363; 3 vouchers, HWML 23397; 13 vouchers (present collection), USNPC 86105, 86106, 86107.

MEASUREMENTS: Body length 270 (n = 1), greatest width 104 (n = 1); haptoral length 66 (n = 1), width 108 (n = 1); pharyngeal diameter



Figures 4–37. Sclerotized structures of *Notothecium* spp. 4–11. *Notothecium mizellei* Boeger and Kritsky, 1988. 4. Ventral anchor. 5. Dorsal anchor. 6. Copulatory complex (ventral view). 7. Hook pair 7. 8. Hook pair 5. 9. Hook pair 1. 10. Ventral bar. 11. Dorsal bar. 12–19. *Notothecium circellum sp. n.* (from *Serrasalmus gouldingi*). 12. Copulatory complex (ventral view). 13. Hook pair 7. 14. Hook pair 5. 15. Hook pair 2. 16. Ventral bar. 17. Dorsal bar. 18. Ventral anchor. 19. Dorsal anchor. 20–28. *Notothecium cyphophallum* sp. n. (from *Serrasalmus rhombeus*). 20. Ventral anchor. 21. Dorsal anchor. 22. Copulatory complex (ventral view). 23. Hook pair 1. 24. Hook pair 2. 25. Hook pair 5. 26. Hook pair 7. 27. Ventral bar. 28. Dorsal bar. 29–37. *Notothecium deleastoideum* sp. n. 29. Copulatory complex (ventral view). 30. Ventral bar. 31. Dorsal bar. 32. Hook pair 1. 33. Hook pair 2. 34. Hook pair 5. 35. Hook pair 7. 36. Ventral anchor. 37. Dorsal anchor. All drawings are to the 25-μm scale.

18 (n = 1); ventral anchor length 50 (48–54; n = 10), base width 21 (17–23; n = 10); dorsal anchor length 47 (46–50; n = 7), base width 18 (15–20; n = 6); ventral bar 37 (n = 1), dorsal bar 31 (n = 1) long; hook pair 1—28 (27–31; n = 5), pair 2—29–30 (n = 2), pair 3—34 (32–37; n = 8), pair 4—34 (31–36; n = 9), pair 5—17 (16–18; n = 6), pair 6—26 (25–28; n = 9), pair 7—36 (33–38; n = 5) long; copulatory organ 27 (25–31; n = 7) long, accessory piece 27 (25–29; n = 10) long; testis 56 (n = 1) long, 32 (n = 1) wide; germarium 57 (n = 1) long, 32 (n = 1) wide.

REMARKS: *Notothecium mizellei* was designated the type species for the genus by Boeger and Kritsky (1988). Our specimens did not differ from those used in the original description. In *N. mizellei,* the subterminal pouch of the vagina lacks a ventral aperture. *Notothecium mizellei* is the only member of the genus with 2 rami of the copulatory organ.

Notothecium circellum sp. n. (Figs. 1, 12–19)

TYPE HOST AND LOCALITY: *Serrasalmus gouldingi:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORD: *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988).

SPECIMENS STUDIED: Holotype, INPA PLH 308; 22 paratypes, INPA PLH 309, USNPC 86108, HWML 38754. 1 voucher from *Pristobrycon* sp., USNPC 86237.

COMPARATIVE MEASUREMENTS: Measurements of the specimen from *Pristobrycon* sp. follow those of the type series in brackets.

DESCRIPTION: Body 340 (285–380; n = 10) long; cephalic region originating anteroventrally from trunk; greatest width 131 (110–159; n = 11) usually in anterior trunk. Tegument smooth. Cephalic lobes moderately developed. Accessory eye granules usually absent, infrequently in cephalic, trunk regions. Pharynx spherical, 20 (18–22; n = 11) in diameter. Peduncle broad; haptor 79 (71–87; n = 11) long, 114 (103–129; n = 11) wide. Anchors similar; each with elongate depressed superficial root, prominent deep root, elongate shaft, short point. Ventral anchor 52 (49–55; n = 12) [48 (n = 1)] long, base 21 (19–23; n = 12) [22 (n = 1)] wide; dorsal anchor 51 (49–53; n = 10) [48 (n = 1)] long, base 17–18 (n = 4) [17 (n = 1)] wide. Ventral bar 37 (36–40; n = 9) long, U-shaped, with slightly enlarged terminations, subterminal anterior expansions; dorsal bar 35 (33–38; n = 10) long, V-shaped, with slightly enlarged ends. Hook pair 1—25 (23–27; n = 4), pair 2—31 (29–33; n = 9), pair 3—36 (34–39; n = 10), pair 4—39 (37–41; n = 11), pair 5—18 (16–23; n = 9), pair 6—27 (25–29; n = 10), pair 7—42 (39–45; n = 12) long. Copulatory organ 77 (70–83; n = 10) [60 (n = 1)] long, coiled (counterclockwise), with about 1 ring, distally sigmoid; base with sclerotized margin, small proximal flap; coil diameter 23 (21–27; n = 11). Distal rod of accessory piece 25 (18–27; n = 12) long, with terminal hook, subterminal thumb. Gonads ovate; testis 62 (54–74; n = 4) long, 27 (22–33; n = 4) wide; germarium 61 (56–66; n = 9) long, 28 (20–34; n = 9) wide. Seminal vesicle a slight dilation of vas deferens. Oviduct, ootype not observed; uterus delicate; vagina usually expanded into spherical chamber (seminal receptacle) proximally, slightly expanded along remaining length, bifurcating distally; sinistroventral branch open.

REMARKS: *Notothecium circellum* is the only species in the genus with a coiled copulatory organ. The specific name is from Latin (*circellus* ["a small ring"]) and refers to the copulatory organ.

Notothecium cyphophallum sp. n. (Figs. 2, 20–28)

TYPE HOST AND LOCALITY: *Serrasalmus rhombeus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORDS: *Pristobrycon eigenmanni:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Negro near Manaus, Amazonas (28 December 1988). *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus compressus:* Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus elongatus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus gouldingi:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus rhombeus:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus* sp. (2 of Jégu): Rio Uatumã, Lago Tapaná, Santana, Amazonas (3 November 1989). *Serrasalmus* sp. (2n = 58):

Furo do Catalão, Manaus, Amazonas (30 January 1991).

SPECIMENS STUDIED: Holotype, INPA PLH 310; 20 paratypes, INPA PLH 311, USNPC 86109, 86110, 86111, HWML 38755 from *S. rhombeus*. Eleven vouchers from *P. eigenmanni,* USNPC 86116, 86117; 1 voucher from *Pristobrycon* sp., USNPC 86112; 3 vouchers from *S. compressus,* USNPC 86113; 10 vouchers from *S. elongatus,* USNPC 86114, 86115; 14 vouchers from *S. gouldingi,* USNPC 86118; 8 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 86119; 6 vouchers from *Serrasalmus* sp. ($2n$ = 58), USNPC 86120.

COMPARATIVE MEASUREMENTS: Table 1.

DESCRIPTION: Greatest body width in posterior trunk. Tegument usually smooth or infrequently with poorly developed scaled annulations on peduncle. Cephalic lobes moderately developed. Accessory eye granules usually in cephalic, anterior trunk regions, infrequently arranged in clusters. Pharynx spherical. Peduncle broad. Anchors similar; each with well-differentiated deep root, depressed superficial root, curved elongate shaft, short point. Ventral bar broadly U-shaped, with terminal enlargements; dorsal bar broadly U- or V-shaped. Copulatory organ tubular, arcuate, with elongate subterminal opening; base with prominent proximal flap. Distal rod of accessory piece sigmoid, with thumb reduced to inconspicuous keel. Gonads subovate; seminal vesicle prominent; single prostatic reservoir; oviduct short; ootype, uterus not observed; vagina distally bifurcate with sinistrodorsal and sinistroventral apertures, dilated, apparently serving as sperm reservoir; seminal receptacle absent; vitellaria limited in trunk, absent in regions of reproductive organs.

REMARKS: *Notothecium cyphophallum* is easily separated from congeners by the morphology of the copulatory organ and its elongate diagonal opening. The specific name is from Greek (*kyphos* ["humped, sloped, curved"] + *phallos* ["penis"] and refers to the shape of the copulatory organ.

Notothecium deleastoideum sp. n. (Figs. 3, 29–37)

TYPE HOST AND LOCALITY: *Serrasalmus* sp. ($2n$ = 58): Furo do Catalão, Manaus, Amazonas (5 January 1989; 30 January 1991).

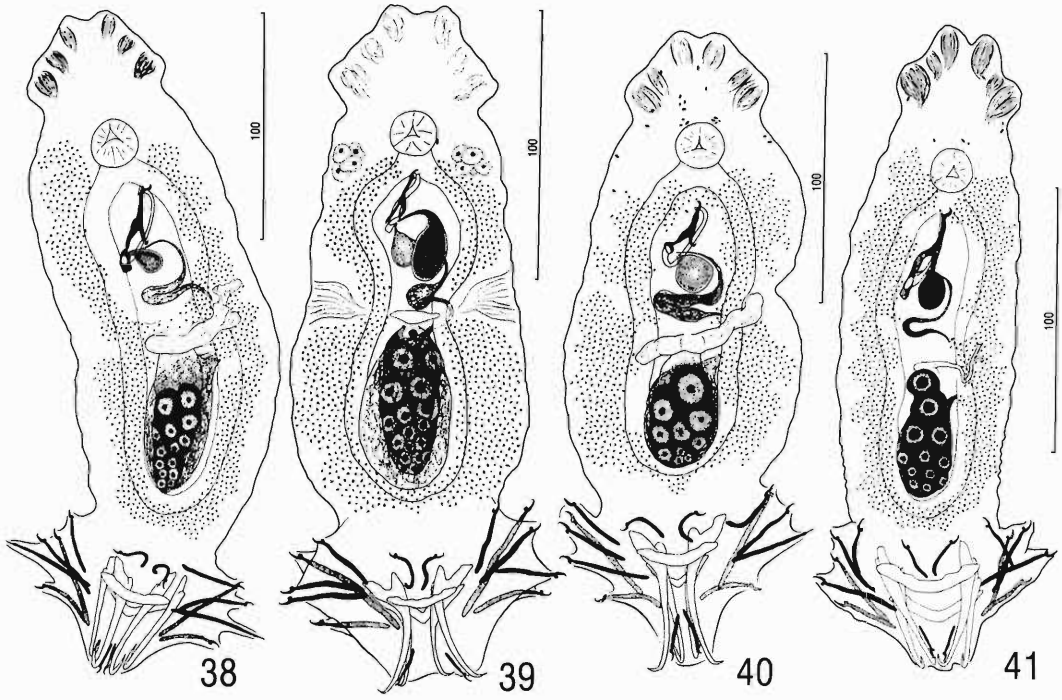
SPECIMENS STUDIED: Holotype, INPA PLH 312; 7 paratypes, INPA PLH 313, USNPC 86121, 86122, HWML 38756.

DESCRIPTION: Body broad, 259 (224–294; n = 2) long; greatest width 99 (85–113; n = 2) near midlength. Tegument smooth or with scaled annulations over posterior half of trunk, peduncle. Cephalic lobes moderately developed. Accessory eye granules present in cephalic, trunk regions, infrequently absent. Pharynx spherical, 18 (16–20; n = 2) in diameter. Peduncle broad to nonexistent; haptor 57 (56–58; n = 2) long, 96 (78–114; n = 2) wide. Anchors similar; each with elongate depressed superficial root, prominent deep root, elongate shaft, short point. Ventral anchor 45 (43–46; n = 6) long, base 19 (17–22; n = 6) wide; dorsal anchor 43 (41–44; n = 4) long, base 16 (14–18; n = 4) wide. Ventral bar 36–37 (n = 2) long, gently curved, with slightly enlarged terminations; dorsal bar 34–35 (n = 2) long, broadly V-shaped, with slightly enlarged ends. Hook pair 1—22 (21–23; n = 5), pair 2—29 (26–30; n = 4), pair 3—33 (32–35; n = 5), pair 4—37 (35–38; n = 4), pair 5—15 (14–16; n = 4), pair 6—24 (23–26; n = 4), pair 7—38 (37–41; n = 5) long. Copulatory organ 37 (35–38; n = 6) long, a broad arced tube terminating short of tip of accessory piece; base with sclerotized margin, small proximal flap. Distal rod of accessory piece 31 (27–33; n = 6) long, with terminal hook, short subterminal thumb. Testis not observed; germarium 43 (36–51; n = 2) long, 33 (28–38; n = 2) wide, subovate. Seminal vesicle prominent. Single prostatic reservoir; oviduct, ootype, uterus not observed; vagina dilated, with sinistrodorsal, sinistroventral openings; seminal receptacle absent; vitellaria in trunk except absent in regions of reproductive organs.

REMARKS: *Notothecium deleastoideum* is similar to *N. reduvium* sp. n. and *N. deleastum* sp. n. in the general morphology of the male copulatory organ. It differs from *N. reduvium* by having less taper of the copulatory organ (copulatory organ tapering to a fine tube in *N. reduvium*) and by the comparative size of the anchors, bars, and hooks (smaller in *N. reduvium*). It differs from *N. deleastum* by having a short copulatory organ (copulatory organ flared distally and extending past the hook of the accessory piece in *N. deleastum*). In *N. deleastum,* the subterminal vaginal pouch is blind (open in *N. deleastoideum*). The specific name reflects the

Table 1. Comparative measurements (in micrometers) of *Notothecium cyphophallum* sp. n., from 8 serrasalmid hosts.

	Pristobrycon eigenmanni	*n*	*Pristobrycon* sp.	*n*	*Serrasalmus compressus*	*n*	*Serrasalmus elongatus*	*n*	*Serrasalmus gouldingi*	*n*	*Serrasalmus rhombeus*	*n*	*Serrasalmus* sp. (2*n* = 58)	*n*	*Serrasalmus* sp. (2 of Jégu)	*n*
Body																
Length	258 (229–288)	2	—	—	—	—	346 (310–376)	3	329 (305–359)	6	284 (189–329)	9	233	1	—	—
Width	66 (62–71)	2	—	—	—	—	86 (81–94)	3	121 (99–148)	6	98 (92–106)	9	107	1	—	—
Haptor																
Length	72 (65–80)	2	—	—	—	—	87 (83–92)	3	81 (78–85)	6	73 (61–80)	9	69	1	—	—
Width	88 (78–98)	2	—	—	—	—	103 (89–120)	3	128 (114–143)	6	111 (104–124)	9	103	1	—	—
Pharynx																
Diameter	16	2	—	—	—	—	17 (15–18)	3	20 (18–23)	6	19 (15–21)	9	19	1	—	—
Copulatory organ																
Length	42 (40–44)	9	—	—	43–44	3	42 (38–46)	6	44 (42–48)	8	43 (41–45)	10	43 (39–46)	5	42 (40–45)	7
Accessory piece																
Length	26 (25–28)	9	26	1	26	3	27 (26–30)	6	27 (25–29)	8	27 (25–30)	11	27 (26–28)	5	25 (24–27)	7
Dorsal anchor																
Length	43 (40–49)	9	43	1	49 (48–50)	2	52 (46–56)	6	49 (46–51)	7	47 (41–50)	8	44 (42–45)	2	47 (43–50)	6
Base width	17 (15–18)	8	15	1	16	1	18 (15–21)	3	18 (17–20)	3	17 (16–18)	6	17–18	2	18 (16–20)	5
Ventral anchor																
Length	49 (45–55)	9	46	1	55 (54–56)	2	57 (54–62)	6	53 (50–57)	7	51 (44–54)	11	49 (48–51)	2	50 (47–56)	7
Base width	22 (20–23)	8	21	1	20 (19–21)	2	21 (18–24)	6	23 (22–25)	7	22 (20–23)	9	22 (21–23)	2	21 (19–22)	7
Bar length																
Ventral	37 (36–38)	2	—	—	—	—	40	2	42 (38–48)	6	39 (31–43)	8	38	1	—	—
Dorsal	34–35	2	—	—	—	—	37–38	2	38 (36–40)	6	38 (36–41)	6	34	1	—	—
Hook lengths																
Pair 1	23 (22–24)	6	22	1	24	1	25 (24–26)	3	29	1	23 (21–24)	3	24–25	2	22	1
Pair 2	29 (27–30)	8	—	—	30	1	31 (26–34)	6	33 (31–37)	6	30 (28–34)	8	30–31	2	29 (27–31)	4
Pair 3	34 (32–36)	8	35	1	35	1	38 (35–40)	6	37 (36–39)	8	37 (32–43)	5	36	2	35 (34–37)	6
Pair 4	38 (36–41)	8	38	1	37	2	41 (37–43)	6	42 (40–43)	8	38 (34–41)	8	40 (38–41)	2	38 (33–41)	7
Pair 5	18	6	18	1	19	1	19 (18–20)	5	19 (18–20)	7	18 (17–19)	6	18	2	18 (17–19)	6
Pair 6	27 (25–29)	9	25	1	25	1	29 (28–30)	4	29	3	26 (25–27)	6	28	2	27 (26–28)	6
Pair 7	41 (40–42)	9	42	1	39 (38–40)	2	45 (41–48)	6	47 (45–49)	6	42 (39–44)	6	42	2	43 (38–47)	7
Germarium																
Length	43 (40–47)	2	—	—	—	—	69 (64–74)	3	63 (56–70)	5	58 (43–76)	7	42	1	—	—
Width	23 (20–26)	2	—	—	—	—	27 (22–32)	3	33 (30–36)	5	26 (19–32)	7	29	1	—	—
Testis																
Length	52 (49–54)	2	—	—	—	—	62 (61–63)	2	71 (54–95)	4	56 (46–68)	5	50	1	—	—
Width	30–31	2	—	—	—	—	26 (25–28)	2	44 (37–63)	4	38 (32–44)	4	38	1	—	—



Figures 38–41. Whole mount illustrations of *Notothecium* spp. (composite, ventral views). 38. *Notothecium deleastum* sp. n. (from *Serrasalmus rhombeus*). 39. *Notothecium modestum* sp. n. 40. *Notothecium phyleticum* sp. n. 41. *Notothecium reduvium* sp. n. (from *Serrasalmus* sp. [2*n* = 58]). All drawings are to respective 100-μm scales.

presumed relationship of this species with *N. deleastum.*

Notothecium deleastum sp. n. (Figs. 38, 42–50)

TYPE HOST AND LOCALITY: *Serrasalmus rhombeus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

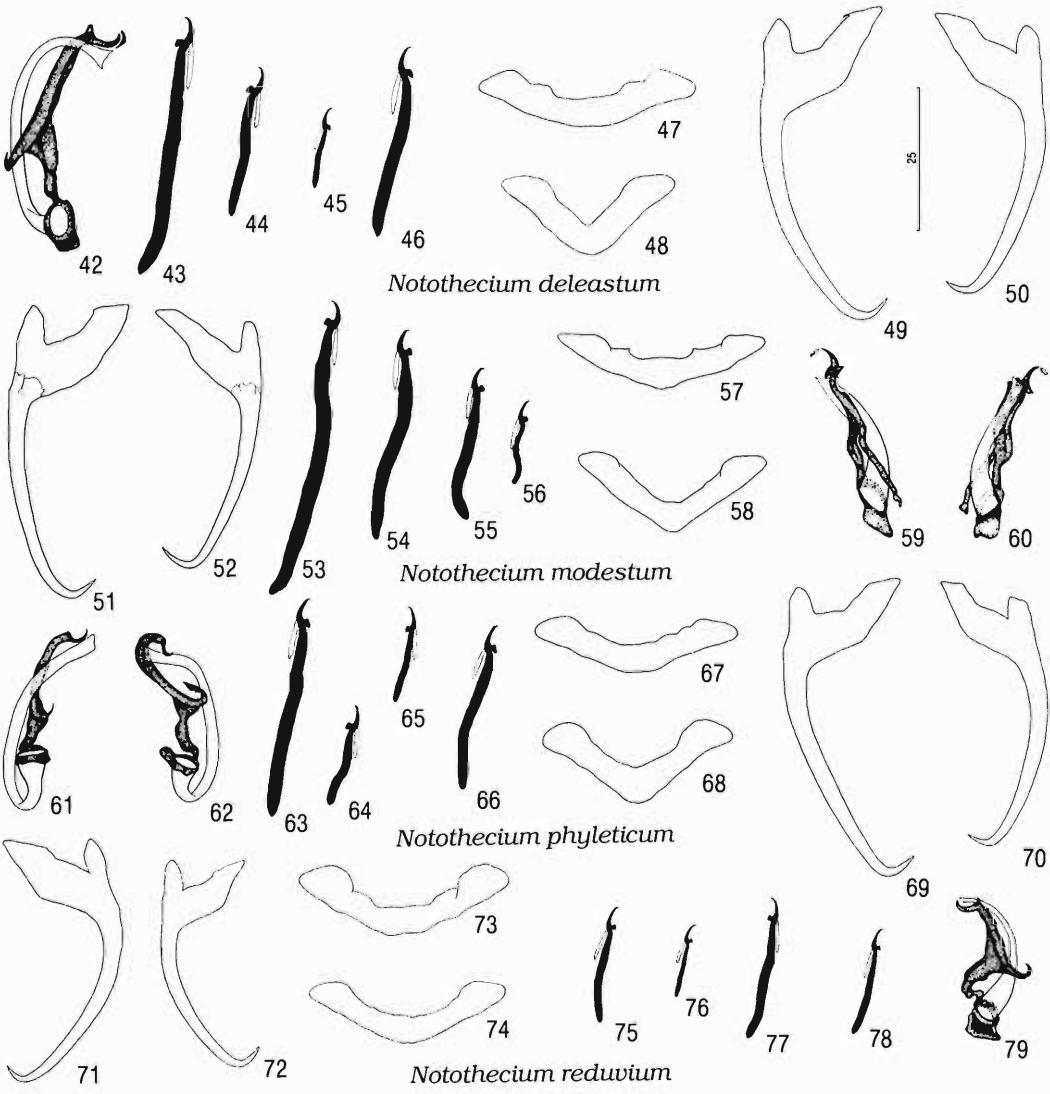
OTHER RECORDS: *Serrasalmus elongatus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus gouldingi:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus* sp. (2*n* = 58): Furo do Catalão, Manaus, Amazonas (5 January 1989; 30 January 1991).

SPECIMENS STUDIED: Holotype, INPA PLH 314; 10 paratypes, INPA PLH 315, USNPC 86125, HWML 38757 from *S. rhombeus.* 10 vouchers from *S. elongatus,* USNPC 86123, 86124; 17 vouchers from *S. gouldingi,* USNPC 86128; 4 vouchers from *Serrasalmus* sp. (2*n* = 58), USNPC 86126, 86127.

COMPARATIVE MEASUREMENTS: Table 2.

DESCRIPTION: Greatest width of body usually in posterior trunk. Tegument smooth. Cephalic lobes moderately developed. Accessory eye granules present in cephalic, trunk regions, infrequently absent. Pharyn spherical. Peduncle broad. Anchors similar; each with depressed superficial root, prominent deep root, elongate shaft, short point. Ventral bar gently curved, with slightly enlarged terminations, subterminal anterior expansions; dorsal bar V-shaped, with slightly enlarged ends. Copulatory organ a broadly U-shaped tube with slightly flared end; base with sclerotized margin, small proximal flap. Distal rod of accessory piece with terminal hook flexed dorsally, short subterminal thumb. Gonads subovate; seminal vesicle delicate. Single prostatic reservoir; oviduct, ootype, uterus not observed; vagina opening sinistrodorsally, expanded, with subterminal blind ventral pouch; seminal receptacle absent; vitellaria in trunk except absent in regions of reproductive organs.

REMARKS: This species resembles *Noto-*



Figures 42–79. Sclerotized structures of *Notothecium* spp. 42–50. *Notothecium deleastum* sp. n. (from *Serrasalmus rhombeus*). 42. Copulatory complex (ventral view). 43. Hook pair 7. 44. Hook pair 1. 45. Hook pair 5. 46. Hook pair 2. 47. Ventral bar. 48. Dorsal bar. 49. Ventral anchor. 50. Dorsal anchor. 51–60. *Notothecium modestum* sp. n. 51. Ventral anchor. 52. Dorsal anchor. 53. Hook pair 7. 54. Hook pair 3. 55. Hook pair 6. 56. Hook pair 5. 57. Ventral bar. 58. Dorsal bar. 59. Copulatory complex (ventral view). 60. Copulatory complex (dorsal view). 61–70. *Notothecium phyleticum* sp. n. 61. Copulatory complex (dorsal view). 62. Copulatory complex (ventral view). 63. Hook pair 7. 64. Hook pair 1. 65. Hook pair 5. 66. Hook pair 3. 67. Ventral bar. 68. Dorsal bar. 69. Ventral anchor. 70. Dorsal anchor. 71–79. *Notothecium reduvium* sp. n. (from *Serrasalmus* sp. [$2n = 58$]). 71. Ventral anchor. 72. Dorsal anchor. 73. Ventral bar. 74. Dorsal bar. 75. Hook pair 2. 76. Hook pair 5. 77. Hook pair 7. 78. Hook pair 1. 79. Copulatory complex (ventral view). All drawings are to the 25-μm scale.

thecium deleastoideum sp. n., from which it differs by having a longer copulatory organ and a blind subterminal vaginal pouch. The specific name is from Greek (*deleastikos* ["enticing"]).

Notothecium modestum sp. n. (Figs. 39, 51–60)

TYPE HOST AND LOCALITY: *Serrasalmus spilopleura:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989).

Table 2. Comparative measurements (in micrometers) of *Notothecium deleastum* sp. n., from 4 serrasalmid hosts.

	Serrasalmus elongatus	*n*	*Serrasalmus gouldingi*	*n*	*Serrasalmus rhombeus*	*n*	*Serrasalmus* sp. (2*n* = 58)	*n*
Body								
Length	250	1	316 (291–331)	6	265 (217–294)	5	265	1
Width	85	1	118 (94–127)	6	91 (83–98)	5	106	1
Haptor								
Length	72	1	73 (67–82)	6	72 (68–80)	5	67	1
Width	101	1	125 (96–153)	6	105 (85–114)	5	96	1
Pharynx								
Diameter	15	1	21 (18–22)	6	19 (17–21)	5	20	1
Copulatory organ								
Length	40 (35–43)	8	38 (35–46)	11	42 (36–52)	6	43 (42–46)	3
Accessory piece								
Length	32 (30–34)	8	32 (29–38)	11	31 (24–35)	6	28 (26–30)	3
Dorsal anchor								
Length	54 (48–57)	6	49 (44–53)	9	49 (45–52)	4	46 (45–48)	3
Base width	15	1	17 (14–20)	7	18–19	2	12	1
Ventral anchor								
Length	56 (51–57)	7	51 (49–56)	11	55 (49–61)	4	50 (47–52)	3
Base width	20 (18–24)	6	21 (17–25)	10	20–21	4	20 (18–21)	3
Bar length								
Ventral	40	1	36 (34–37)	5	35 (33–39)	4	—	—
Dorsal	35	1	32 (30–34)	5	31 (29–33)	4	—	—
Hook lengths								
Pair 1	26	1	22	1	26	1	—	—
Pair 2	33 (31–36)	2	30 (28–33)	7	31 (28–34)	2	29	2
Pair 3	37 (36–39)	4	35 (33–40)	10	37 (35–40)	2	34 (33–35)	3
Pair 4	42 (39–44)	7	39 (35–42)	11	38 (35–41)	5	36	3
Pair 5	17 (16–18)	5	17 (16–19)	15	17	3	15 (14–17)	2
Pair 6	28 (27–29)	4	27 (26–31)	6	27 (26–28)	2	25	1
Pair 7	46 (45–49)	4	46 (42–52)	9	46 (43–49)	4	38 (34–41)	3
Germarium								
Length	39	1	52 (45–60)	5	44 (38–46)	5	—	—
Width	25	1	30 (23–39)	5	21 (19–22)	5	—	—
Testis								
Length	—	—	59 (52–69)	3	48 (44–50)	3	—	—
Width	—	—	31 (28–35)	3	27 (19–33)	3	—	—

OTHER RECORDS: *Serrasalmus spilopleura:* Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (14 September 1984); Furo do Catalão, Manaus, Amazonas (2 November 1993).

SPECIMENS STUDIED: Holotype, INPA PLH 316; 56 paratypes, INPA PLH 317, PLH 318, USNPC 86130, 86131, HWML 38758; 3 vouchers, USNPC 86129.

DESCRIPTION: Body 257 (222–294; $n = 21$) long, with bilateral subtriangular zones lacking vitellaria near midlength of trunk; greatest width 102 (89–119; $n = 23$) in posterior trunk. Tegument smooth. Cephalic margin broad; cephalic lobes moderately developed. Accessory eye granules uncommon in cephalic, anterior trunk regions. Pharynx spherical, 17 (15–18; $n = 24$) in diameter. Peduncle broad; haptor 70 (60–83; $n = 23$) long, 102 (85–117; $n = 21$) wide. Anchors similar; each with elongate deep root, depressed superficial root, delicate shaft, short point; ventral anchor 50 (47–53; $n = 30$) long, base 19 (16–22; $n = 30$) wide; dorsal anchor 47 (43–52; $n = 28$) long, base 17 (14–19; $n = 21$) wide. Ventral bar 36 (34–38; $n = 20$) long, broadly V-shaped, with irregular anterior margin. Dorsal bar 30 (28–33; $n = 15$) long, V-shaped, with slightly enlarged ends. Hook pairs 1, 6—26 (22–30; $n = 26$); pair 2—32 (29–37; $n = 10$); pairs 3, 4—37 (33–41; $n = 57$); pair 5—15 (14–17; $n = 23$); pair 7—52 (45–59; $n =$

27) long. Copulatory organ 30 (29–32; n = 17) long, a tapered sigmoid tube; base of copulatory organ with sclerotized margin, small proximal flap. Distal rod of accessory piece 31 (29–33; n = 23) long, with terminal hook, subterminal thumb. Testis 47 (39–54; n = 7) long, 29 (25–35; n = 7) wide, elongate ovate; seminal vesicle fusiform, C-shaped, lying in left side of trunk; prostatic reservoirs pyriform. Germarium ovate, 44 (34–56; n = 19) long, 27 (17–38; n = 19) wide; oviduct, ootype, uterus, vagina, seminal receptacle not observed; vitellaria dense throughout trunk except absent in regions of reproductive organs.

REMARKS: The bilateral triangular zones lacking vitellaria near the midlength of the trunk may represent positions of vaginal apertures, but apertures and vaginal ducts, primary characters for generic assignment of ancyrocephalines parasitizing serrasalmids, could not be determined in available specimens. Thus, we assign this species to *Notothecium* based on the slight dorsoventral flattening of the body, the absence of eyes, and the general morphology of the copulatory complex and haptoral structures. In *N. modestum,* the C-shaped seminal vesicle is limited to the left side of the trunk, while the seminal vesicle of all other congeneric species extends into the right side. The specific name is from Latin (*modestus* ["unassuming"]).

Notothecium phyleticum sp. n. (Figs. 40, 61–70)

TYPE HOST AND LOCALITY: *Serrasalmus rhombeus:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989).

OTHER RECORDS: *Serrasalmus rhombeus:* Rio Capucapú at its confluence with Rio Jatapú, Cachoeira das Garças, Amazonas (31 October 1989); Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 319; 7 paratypes, INPA PLH 320, USNPC 86132, 86133, 86134, HWML 38759.

DESCRIPTION: Body broad, 245 (195–282; n = 3) long; greatest width 96 (84–103; n = 3) usually in posterior trunk. Tegument smooth. Cephalic lobes moderately developed. Accessory eye granules usually present in cephalic, anterior trunk regions. Pharynx spherical, 18 (17–19; n = 3) in diameter. Peduncle broad; haptor 73 (64–78; n = 3) long, 92 (81–99; n = 3) wide. Anchors similar; each with depressed superficial root, prominent deep root, elongate shaft, short point; ventral anchor 51 (46–56; n = 5) long, base 19 (17–20; n = 5) wide; dorsal anchor 49 (47–51; n = 5) long, base 14 (11–17; n = 4) wide. Ventral bar 31 (28–34; n = 3) long, bent near midlength, with slightly enlarged terminations; dorsal bar 31–32 (n = 3) long, V-shaped, with enlarged ends. Hook pair 1—22 (21–24; n = 4), pair 2—26 (20–31; n = 5), pair 3—31 (29–33; n = 5), pair 4—34 (32–36; n = 5), pair 5—16–17 (n = 5), pair 6—24 (23–25; n = 5), pair 7—41 (39–43; n = 5) long. Copulatory organ 35 (29–40; n = 5) long, J-shaped; base with sclerotized margin, small proximal flap occasionally absent. Distal rod of accessory piece 20 (17–23; n = 5) long, C-shaped, with terminal hook, small subterminal thumb. Gonads ovate to subspherical; testis 38 (n = 1) long, 24 (n = 1) wide; germarium 46 (n = 1) long, 23 (n = 1) wide. Seminal vesicle moderately developed. Single prostatic reservoir; oviduct, ootype, uterus not observed; vagina dilated, opening by indistinct slit on sinistrodorsal surface of trunk; ventral pouch poorly developed, blind; dextral vaginal branch present, blind; seminal receptacle absent; vitellaria limited in trunk, absent in regions of reproductive organs.

REMARKS: *Notothecium phyleticum* resembles several species of *Notothecium* including *N. reduvium* sp. n., *N. deleastum* sp. n., *N. deleastoideum* sp. n., *N. mizellei* Boeger and Kritsky, 1988, and *N. cyphophallum* sp. n. by the general morphology of the copulatory complex. It is distinguished from these species by having a J-shaped copulatory organ and a dextral vaginal branch. The specific name is from Greek (*phyletes* ["one of the same tribe"]).

Notothecium reduvium sp. n. (Figs. 41, 71–79)

TYPE HOST AND LOCALITY: *Serrasalmus* sp. ($2n$ = 58): Furo do Catalão, Manaus, Amazonas (5 January 1989; 30 January 1991).

OTHER RECORDS: *Serrasalmus* sp. (2 of Jégu): Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 321; 12 paratypes, INPA PLH 322, USNPC 86137, 86138, HWML 38760. 7 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 86135, 86136.

COMPARATIVE MEASUREMENTS: Measurements

of specimens from *Serrasalmus* sp. (2 of Jégu) follow those of the type series in brackets.

DESCRIPTION: Body 245 (244–246; $n = 2$) long; greatest width 85 (75–95; $n = 2$) near midlength. Tegument smooth. Cephalic lobes moderately developed. Accessory eye granules usually present in cephalic, anterior trunk regions. Pharynx spherical, 16 (14–18; $n = 2$) in diameter. Peduncle broad; haptor 68 (67–69; $n = 2$) long, 90 (85–95; $n = 2$) wide. Anchors similar; each with depressed superficial root, prominent deep root, elongate shaft, short point; ventral anchor 46 (43–50; $n = 10$) [43 (41–45; $n = 7$)] long, base 17 (15–19; $n = 11$) [17 (16–19; $n = 7$)] wide; dorsal anchor 39 (36–43; $n = 6$) [40 (37–43; $n = 6$)] long, base 13 (11–15; $n = 7$) [13–14 ($n = 3$)] wide. Ventral bar 35 ($n = 2$) long, broadly U-shaped, with enlarged terminations; dorsal bar 32 ($n = 1$) long, U- or V-shaped, with slightly enlarged ends. Hook pair 1—22 (21–24; $n = 7$) [19 (18–21; $n = 3$)], pair 2—24 (21–25; $n = 7$) [23 (22–25; $n = 5$)], pair 3—30 (27–31; $n = 9$) [28 (26–30; $n = 6$)], pair 4—33 (30–36; $n = 9$) [32 (31–33; $n = 6$)], pair 5—15–16 ($n = 8$) [16–17 ($n = 6$)], pair 6—23 (22–24; $n = 8$) [23 (21–24; $n = 7$)], pair 7—29 (26–32; $n = 9$) [27 (23–30; $n = 7$)] long. Copulatory organ 28 (26–31; $n = 7$) [29 (26–32; $n = 6$)] long, tapered; base with sclerotized margin, short proximal flap. Distal rod of accessory piece 21 (19–23; $n = 11$) [20 (17–21; $n = 5$)] long, with terminal hook, short subterminal thumb. Gonads subovate to pyriform; testis 42 (40–44; $n = 2$) long, 23–24 ($n = 2$) wide; germarium 50 ($n = 1$) long, 20 ($n = 1$) wide. Seminal vesicle a slight dilation of vas deferens. Single prostatic reservoir; oviduct, ootype, uterus not observed; vagina slightly dilated, bifurcated distally, with sinistroventral, sinistrodorsal apertures; seminal receptacle absent; vitellaria in trunk except absent in regions of reproductive organs.

REMARKS: This species resembles *Notothecium deleastum* sp n. and *N. deleastoideum* sp. n., from which it differs by having a more delicate tapered copulatory organ. The specific name is from Latin (*reduvia* ["a hangnail"]) and refers to the tip of the accessory piece.

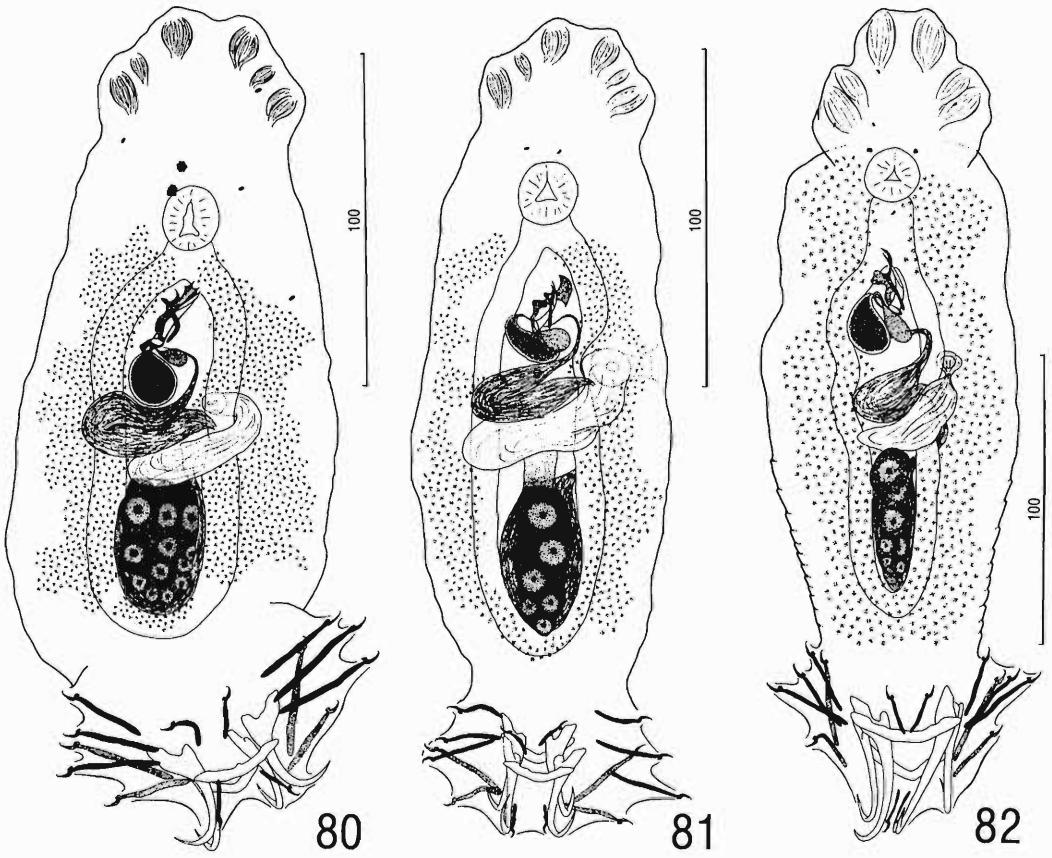
Enallothecium gen. n.

DIAGNOSIS: Body somewhat flattened dorsoventrally; comprising cephalic region, trunk, peduncle, haptor. Tegument thin, smooth, or with scaled annulations. Two terminal, 2 bilateral cephalic lobes; head organs present; cephalic glands unicellular, lateral or posterolateral to pharynx. Eyes poorly developed or absent; granules elongate ovate. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; intestinal ceca 2, confluent posterior to gonads, lacking diverticula. Gonads intercecal, overlapping; testis dorsal to germarium. Vas deferens looping left intestinal cecum; seminal vesicle a C-shaped dilated loop of vas deferens extending into right half of trunk; 2 prostatic reservoirs. Copulatory complex comprising articulated copulatory organ, accessory piece; copulatory organ a short arced tube with diagonal opening. Accessory piece comprising distal rod, proximal articulation process; distal rod with terminal hook, thumb surrounded by poorly sclerotized mass, umbell originating from base of thumb. Seminal receptacle absent; vagina looping left intestinal cecum, dilated, nonsclerotized, opening on papilla lying on sinistrodorsal surface near body midlength. Genital pore midventral near level of intestinal bifurcation. Vitellaria coextensive with intestine. Haptor subhexagonal, with pairs of dorsal and ventral anchor/bar complexes, 7 pairs of hooks with ancyrocephaline distribution. Hooks similar; each with delicate point, truncate protruding thumb, expanded shank comprising two subunits; proximal subunit variable in length between hook pairs. FH loop extending to union of shank subunits. Ventral bar lacking anteromedial process. Parasites of gills of serrasalmid fishes.

TYPE SPECIES: *Enallothecium aegidatum* (Boeger and Kritsky, 1988) comb. n. from *Pristobrycon* sp., *Pygocentrus nattereri* (type host), *Serrasalmus compressus, S. elongatus, S. gouldingi, S. rhombeus, S. spilopleura, Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. ($2n = 58$).

OTHER SPECIES: *Enallothecium cornutum* sp. n. from *Pristobrycon eigenmanni, Pristobrycon* sp., *Serrasalmus compressus, S. gouldingi, S. rhombeus* (type host), *Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. ($2n = 58$); *E. umbelliferum* sp. n. from *S. compressus* and *S. rhombeus* (type host); and *E. variabilum* sp. n. from *P. striolatus.*

REMARKS: The type species of *Enallothecium* was originally placed in *Notothecium* by Boeger and Kritsky (1988). However, the 3 new species described below and *N. aegidatum* appear to form a monophyletic assemblage for

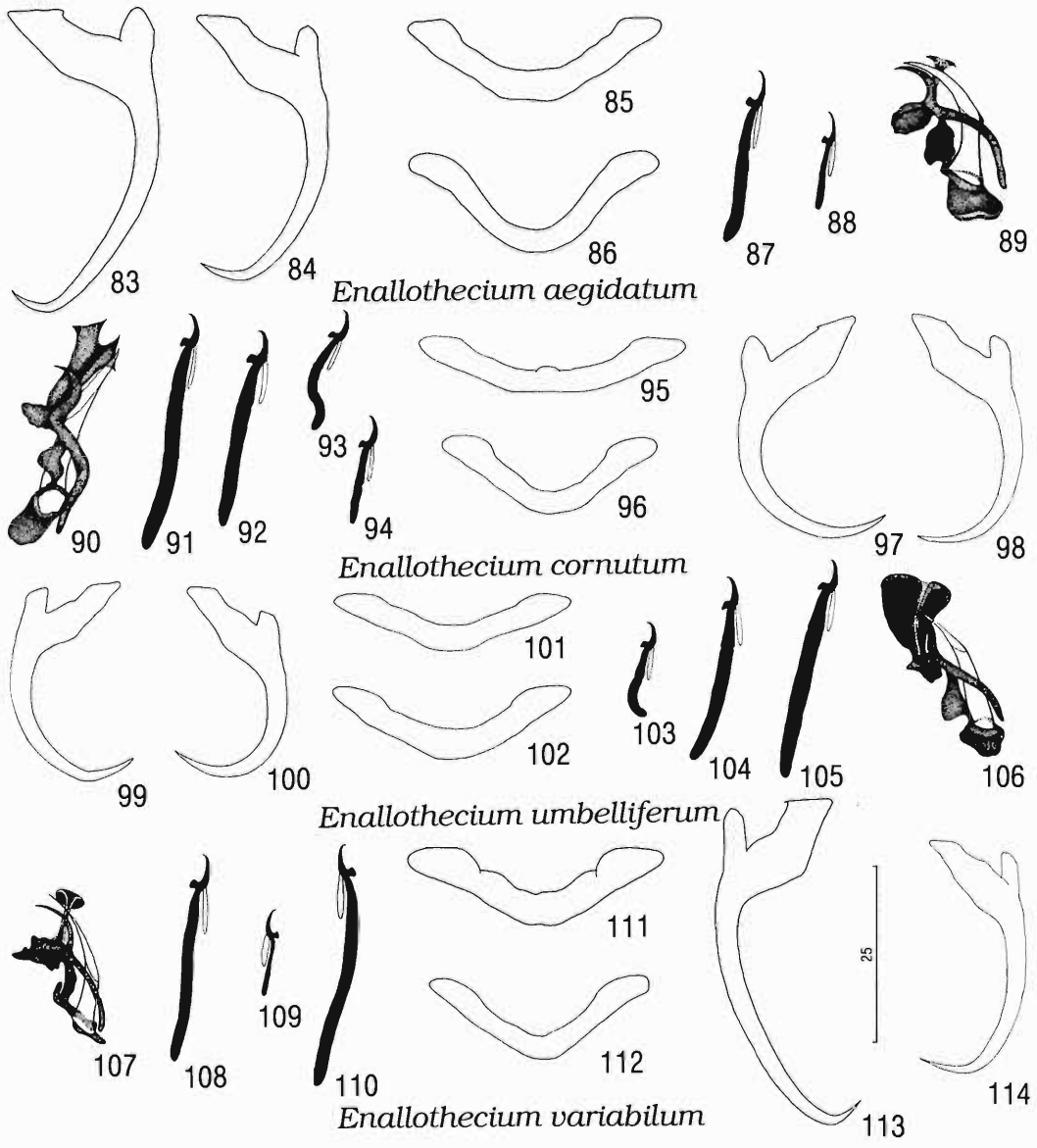


Figures 80–82. Whole mount illustrations of *Enallothecium* spp. (composite, ventral views). 80. *Enallothecium cornutum* sp. n. (from *Serrasalmus rhombeus*). 81. *Enallothecium umbelliferum* sp. n. (from *Serrasalmus rhombeus*). 82. *Enallothecium variabilum* sp. n. All drawings are to respective 100-μm scales.

which *Enallothecium* is proposed. Apparent synapomorphic features of *Enallothecium* include a diagonal opening of the male copulatory organ, presence of an umbell and flap-like thumb of the accessory piece, and the vagina opening at the tip of a small papilla on the sinistrodorsal surface of the trunk.

Enallothecium aegidatum (Boeger and Kritsky, 1988) comb. n. (Figs. 83–89)

RECORDS: *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Pygocentrus nattereri:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Furo do Catalão, Manaus, Amazonas (6 November 1984). *Serrasalmus compressus:* Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (28 October 1993). *Serrasalmus elongatus:* Furo do Catalão, Manaus, Amazonas (27 November 1984); Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus gouldingi:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus rhombeus:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus spilopleura:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (14 September 1984). *Serrasalmus* sp. (2 of Jégu): Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Santa Luzia, Rio Uatumã, Amazonas (20 September 1985). *Serrasalmus* sp. ($2n = 58$): Furo do Catalão, Manaus, Amazonas (5 January 1989, 30 January 1991).



Figures 83–114. Sclerotized structures of *Enallothecium* spp. 83–89. *Enallothecium aegidatum* (Boeger and Kritsky, 1988) (from *Serrasalmus gouldingi*.) 83. Ventral anchor. 84. Dorsal anchor. 85. Ventral bar. 86. Dorsal bar. 87. Hook pair 3. 88. Hook pair 5. 89. Copulatory complex (ventral view). 90–98. *Enallothecium cornutum* sp. n. (from *Serrasalmus rhombeus*). 90. Copulatory complex (ventral view). 91. Hook pair 7. 92. Hook pair 3. 93. Hook pair 1. 94. Hook pair 5. 95. Ventral bar. 96. Dorsal bar. 97. Ventral anchor. 98. Dorsal anchor. 99–106. *Enallothecium umbelliferum* sp. n. (from *Serrasalmus rhombeus*). 99. Ventral anchor. 100. Dorsal anchor. 101. Ventral bar. 102. Dorsal bar. 103. Hook pair 1. 104. Hook pair 3. 105. Hook pair 7. 106. Copulatory complex (ventral view). 107–114. *Enallothecium variabilum* sp. n. 107. Copulatory complex (ventral view). 108. Hook pair 3. 109. Hook pair 5. 110. Hook pair 7. 111. Ventral bar. 112. Dorsal bar. 113. Ventral anchor. 114. Dorsal anchor. All drawings are to the 25-μm scale.

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas (type locality); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia; Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

SPECIMENS STUDIED: 1 voucher from *Pristobrycon* sp., USNPC 86141; 6 vouchers from *Pygocentrus nattereri,* USNPC 86142, 86143; 7 vouchers from *S. compressus,* USNPC 86150; 5 vouchers from *S. elongatus,* USNPC 86144, 86145; 14 vouchers from *S. gouldingi,* USNPC 86151; 11 vouchers from *S. rhombeus,* USNPC 86152, 86153, 86154; 5 vouchers from *S. spilopleura,* USNPC 86139, 86140; 3 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 86146, 86147; 10 vouchers from *Serrasalmus* sp. (2*n* = 58), USNPC 86148, 86149.

COMPARATIVE MEASUREMENTS: Table 3.

REMARKS: *Enallothecium aegidatum* was originally described as *Notothecium aegidatum* from *Pygocentrus nattereri* by Boeger and Kritsky (1988). This species apparently has a wide host tolerance having herein been found on 9 species of *Pristobrycon, Pygocentrus,* and *Serrasalmus.* Although not reported in the original description, *E. aegidatum* does possess a small, weakly sclerotized umbell in the accessory piece. *Enallothecium aegidatum* differs from *E. cornutum* sp. n. and *E. umbelliferum* sp. n. by having anchors with elongate shafts and short points. It differs from *E. variabilum* sp. n. by having a more robust distal rod and a less developed umbell of the accessory piece and by the dorsal anchor being slightly smaller than the ventral anchor (anchors of noticeably different size in *E. variabilum*).

Enallothecium cornutum sp. n. (Figs. 80, 90–98)

TYPE HOST AND LOCALITY: *Serrasalmus rhombeus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORDS: *Pristobrycon eigenmanni:* Rio Negro near Manaus, Amazonas (28 December 1988); Nazaré, Rio Uatumã, Amazonas (17 September 1985). *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus compressus:* Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (28 October 1993). *Serrasalmus gouldingi:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus rhombeus:* Rio Uatumã, Lago Tapaná near Santana, Amazonas (3 November 1989); Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus* sp. (2 of Jégu): Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Nazare, Rio Uatumã, Amazonas (17 September 1985). *Serrasalmus* sp. (2*n* = 58): Furo do Catalão, Manaus, Amazonas (5 January 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 323; 3 paratypes, USNPC 86155, 86156, 86157. 4 vouchers from *P. eigenmanni,* USNPC 86158, 86159; 1 voucher from *Pristobrycon* sp., USNPC 86161; 3 vouchers from *S. compressus,* USNPC 86160; 11 vouchers from *S. gouldingi,* USNPC 86165; 2 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 86163, 86164; 3 vouchers from *Serrasalmus* sp. (2*n* = 58), USNPC 86162.

COMPARATIVE MEASUREMENTS: Table 4.

DESCRIPTION: Greatest body width in posterior trunk. Tegument smooth. Cephalic lobes moderately developed. Eyes usually absent; eye granules variable in size; accessory granules few or absent in cephalic, anterior trunk regions. Pharynx spherical. Peduncle broad. Anchors similar; each with well-developed roots, depressed superficial root, evenly curved shaft, elongate point. Ventral bar broadly U-shaped, with small terminal enlargements, short stubby anteromedial projection infrequently present; dorsal bar broadly U-shaped, with slightly enlarged ends. Copulatory organ slightly arced; base with small proximal flap. Distal rod of accessory piece sigmoid; cornate umbell with 2 terminal, 2 bilateral spines. Gonads subovate; seminal vesicle prominent. Oviduct short; ootype, uterus not observed; vitellaria limited in trunk, absent in regions of reproductive organs.

REMARKS: *Enallothecium cornutum* resembles *E. umbelliferum* sp. n. in the general morphology of the haptoral armament. It differs from this species by having a spined umbell of the accessory piece (umbell large and unspined in *E. umbelliferum*). The specific name is from Latin (*cornutus* ["horned"]) and refers to the spines on the umbell of the accessory piece.

Enallothecium umbelliferum sp. n. (Figs. 81, 99–106)

TYPE HOST AND LOCALITY: *Serrasalmus rhombeus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

Table 3. Comparative measurements (in micrometers) of *Enallothecium aegidatum* (Boeger and Kritsky, 1988) comb. n., from 9 serrasalmid hosts.

	Pristobrycon sp.	*n*	*Pygocentrus nattereri*	*n*	*Serrasalmus compressus*	*n*	*Serrasalmus elongatus*	*n*	*Serrasalmus gouldingi*	*n*	*Serrasalmus rhombeus*	*n*	*Serrasalmus spilopleura*	*n*	*Serrasalmus* sp. (2 of Jégu)	*n*	*Serrasalmus* sp. (2*n* = 58)	*n*
Body																		
Length	—	—	—	—	—	—	—	—	310 (248–388)	7	299 (264–334)	2	270 (229–310)	2	—	—	222 (186–241)	3
Width	—	—	—	—	—	—	—	—	105 (91–122)	7	96	2	82	1	—	—	91 (85–94)	3
Haptor																		
Length	—	—	—	—	—	—	—	—	70 (62–75)	7	72 (58–87)	2	69	1	—	—	59 (55–63)	3
Width	—	—	—	—	—	—	—	—	99 (92–108)	7	102 (98–107)	2	69	1	—	—	91 (85–94)	3
Pharynx																		
Diameter	—	—	—	—	—	—	—	—	19 (16–21)	7	19–20	2	17	1	—	—	15 (14–16)	3
Copulatory organ																		
Length	26	1	23 (21–28)	6	23 (22–24)	3	23 (21–25)	4	25 (23–26)	7	23 (21–24)	5	21–22	2	—	—	23 (22–25)	5
Accessory piece																		
Length	22	1	22 (20–25)	6	21 (20–22)	2	21 (19–22)	4	22 (21–23)	6	20 (19–22)	5	20–21	2	27	1	21 (19–22)	5
Dorsal anchor																		
Length	—	—	36 (32–41)	6	36 (35–37)	6	35 (31–39)	4	39 (38–41)	6	38 (36–40)	7	38 (37–39)	2	34 (31–36)	2	37	2
Base width	—	—	14 (13–16)	5	13–14	2	13 (11–16)	4	16 (14–18)	5	13–14	2	13	2	14	1	14	2
Ventral anchor																		
Length	42	1	40 (36–46)	6	40 (37–41)	6	37 (32–42)	4	43 (42–44)	7	40 (37–43)	8	37–38	3	39 (37–41)	2	39 (36–42)	7
Base width	18	1	17 (14–18)	6	15 (14–16)	5	16 (15–17)	4	19 (18–21)	5	16–17	5	17 (15–18)	3	16 (14–18)	2	16 (15–17)	6
Bar length																		
Ventral	—	—	42	1	—	—	—	—	36 (34–40)	6	37 (35–39)	2	35–36	2	—	—	38 (36–40)	3
Dorsal	—	—	37–38	2	—	—	—	—	33 (30–36)	6	33 (30–37)	2	32 (28–35)	2	—	—	32 (30–35)	3
Hook lengths																		
Pair 1	—	—	22 (21–23)	2	21 (19–22)	4	24 (22–28)	3	22	1	21–22	2	20	1	21 (20–22)	3	21	1
Pair 2	26	1	26	1	24–25	2	24–25	2	27–28	2	27 (26–28)	5	25	1	25 (24–26)	2	24–25	3
Pair 3	34	1	30 (28–31)	5	29 (28–30)	4	29 (27–31)	3	32 (31–34)	5	31 (29–32)	7	31	2	32 (30–34)	2	32 (31–33)	5
Pair 4	31	1	30 (27–31)	5	29 (28–30)	4	29	3	32 (30–33)	5	30 (29–33)	9	29–30	2	33	1	32 (30–34)	5
Pair 5	14	1	16	4	15–16	4	15–16	2	16	4	15	3	15	1	14–15	2	15–16	3
Pair 6	24	1	20–21	2	22 (21–23)	2	20	1	22–23	2	23 (22–25)	5	22	1	21	1	22	1
Pair 7	41	1	33 (31–35)	4	34 (33–35)	4	35 (33–36)	4	39 (37–41)	3	39 (36–44)	5	34 (32–36)	2	39 (38–40)	2	36 (33–40)	5
Germarium																		
Length	—	—	—	—	—	—	—	—	52 (41–61)	6	49 (40–59)	2	43	1	—	—	33 (23–43)	3
Width	—	—	—	—	—	—	—	—	20 (19–23)	6	15 (10–20)	2	8	1	—	—	16–17	3
Testis																		
Length	—	—	—	—	—	—	—	—	54 (52–57)	4	44	1	—	—	—	—	52	1
Width	—	—	—	—	—	—	—	—	28 (25–30)	4	21	1	—	—	—	—	20	1

Table 4. Comparative measurements (in micrometers) of *Enallothecium cornutum* sp. n., from 7 serrasalmid hosts.

	Pristobrycon eigenmanni	*n*	*Pristobrycon* sp.	*n*	*Serrasalmus compressus*	*n*	*Serrasalmus gouldingi*	*n*	*Serrasalmus rhombeus*	*n*	*Serrasalmus* sp. (2 of Jégu)	*n*	*Serrasalmus* sp. (2*n* = 58)	*n*
Body														
Length	201	1	—	—	—	—	314 (291–345)	6	250 (243–256)	2	—	—	265	1
Width	69 (67–71)	2	—	—	—	—	115 (94–135)	6	110 (104–115)	2	—	—	104	1
Haptor														
Length	55	1	—	—	—	—	65 (59–70)	6	57 (45–68)	2	—	—	59	1
Width	64	1	—	—	—	—	108 (96–124)	6	96 (89–102)	2	—	—	85	1
Pharynx														
Diameter	16–17	2	—	—	—	—	20 (19–21)	5	20 (18–21)	2	—	—	19	1
Copulatory organ														
Length	28 (27–29)	2	27	1	25 (24–27)	2	25 (22–29)	4	28–29	2	28	1	22	1
Accessory piece														
Length	24	2	25	1	23	2	23 (21–26)	4	26 (25–28)	2	25	1	—	—
Dorsal anchor														
Length	32 (30–33)	2	31	1	32 (29–33)	3	33 (31–35)	2	33	1	34	3	33	1
Base width	16	2	13	1	11	1	20	2	15	1	17	1	14	1
Ventral anchor														
Length	31–32	2	31	1	30 (29–31)	3	30 (27–33)	5	36 (34–38)	2	30 (28–33)	4	30–31	2
Base width	18–19	2	16	1	17 (16–18)	2	18 (15–21)	3	16–17	2	17 (15–19)	4	20	1
Bar length														
Ventral	29	1	—	—	—	—	37 (30–40)	5	38–39	2	—	—	37	1
Dorsal	26	1	—	—	—	—	33 (31–35)	5	33	2	—	—	33	1
Hook lengths														
Pair 1	18 (17–19)	2	—	—	—	—	22	1	20	1	18	1	18	1
Pair 2	24	1	27	1	24	1	25 (23–29)	4	24–25	2	27	2	24	1
Pair 3	28	1	29	1	28–29	2	27 (24–32)	5	30–31	2	30 (29–31)	2	29	2
Pair 4	28	1	29	1	28–29	2	30 (27–34)	7	30–31	2	31 (29–32)	3	30	1
Pair 5	17	1	16	1	15	1	16 (14–17)	2	16	1	16–17	2	—	—
Pair 6	20 (19–21)	2	24	1	22–23	1	24 (23–25)	3	23	1	23	2	22	2
Pair 7	28 (27–29)	2	33	1	31 (29–33)	2	34–35	3	34 (32–35)	2	32 (30–34)	2	32 (31–33)	2
Germarium														
Length	39	1	—	—	—	—	48 (47–51)	5	43 (40–45)	2	—	—	35	1
Width	15	1	—	—	—	—	28 (20–37)	4	28	2	—	—	23	1
Testis														
Length	—	—	—	—	—	—	52 (46–57)	4	46	1	—	—	—	—
Width	—	—	—	—	—	—	33 (26–44)	4	29	1	—	—	—	—

OTHER RECORDS: *Serrasalmus compressus:* Rio Solimões, Ilha da Marchantaria, Manaus, Amazonas (28 October 1993). *Serrasalmus* sp. (2 of Jégu): Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 324; 9 paratypes, INPA PLH 325, USNPC 86166, HWML 38761. 4 vouchers from *Serrasalmus compressus,* USNPC 86168; 1 voucher from *Serrasalmus* sp. (2 of Jégu), USNPC 86167.

COMPARATIVE MEASUREMENTS: Measurements of specimens from *Serrasalmus compressus* follow those of the type series in brackets. The specimen from *Serrasalmus* sp. (2 of Jégu) was not measured.

DESCRIPTION: Body 266 (243–318; $n = 6$) long; greatest width 94 (78–115; $n = 6$) near midlength. Tegument smooth, infrequently with scaled annulations in posterior trunk, peduncle. Cephalic lobes moderately developed. Accessory eye granules usually present in cephalic, anterior trunk regions. Pharynx spherical, 18 (16–21; $n = 6$) in diameter. Peduncle broad; haptor 57 (50–66; $n = 6$) long, 89 (85–92; $n = 6$) wide. Anchors similar; each with elongate, slightly depressed superficial root, prominent deep root, evenly curved shaft, long point; ventral anchor 28 (26–31; $n = 5$) [30–31 ($n = 3$)] long, base 14 (13–15; $n = 3$) [14 (13–16; $n = 3$)] wide; dorsal anchor 29–30 ($n = 4$) [32 (31–33; $n = 3$)] long, base 15 (14–17; $n = 2$) [13 (11–14; $n = 2$)] wide. Bars similar, broadly U-shaped, with slightly enlarged terminations; ventral bar 32 (29–36; $n = 5$) long, dorsal bar 32 (29–35; $n = 6$) long. Hook pair 1—[16 ($n = 1$)], pair 2—22 (21–24; $n = 3$) [22–23 ($n = 2$)], pair 3—28 (26–29; $n = 4$) [28 ($n = 2$)], pair 4—29 (27–31; $n = 3$) [28 (27–29; $n = 2$)], pair 5—14–15 ($n = 2$) [14 ($n = 2$)], pair 6—19 (18–20; $n = 2$) [21 ($n = 1$)], pair 7—30 (27–32; $n = 3$) [29–30 ($n = 2$)] long. Copulatory organ 23 (21–25; $n = 4$) [26 (25–27; $n = 3$)] long, base with sclerotized margin, small proximal flap. Distal rod of accessory piece 27–28 ($n = 4$) [24–25 ($n = 3$)] long, sigmoid, with terminal hook, subterminal thumb, large umbell. Gonads subovate; testis 46 (41–52; $n = 3$) long, 24 (18–28; $n = 3$) wide; germarium 41 (35–45; $n = 6$) long, 17 (14–21; $n = 6$) wide. Seminal vesicle prominent. Ootype, uterus not observed; vitellaria in trunk except absent in regions of reproductive organs.

REMARKS: *Enallothecium umbelliferum* differs from all other species in the genus by having a large umbell in the accessory piece. The specific name is from Latin (*umbella* ["a sun shade"] + *fero* ["to bear"]) and refers to the umbell of the accessory piece.

Enallothecium variabilum sp. n. (Figs. 82, 107–114)

TYPE HOST AND LOCALITY: *Pristobrycon striolatus:* Rio Capucapú at its confluence with Rio Jatapú, Cachoeira das Garças, Amazonas (31 October 1989).

OTHER RECORDS: *Pristobrycon striolatus:* Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Santa Luzia, Rio Uatumã, Amazonas, (20 September 1985); Lago Samaumá, Rio Uatumã, Amazonas (25 September 1985); Rio Pitinga, Igarapé Agua Branca, Rio Uatumã, Amazonas (15 September 1985).

SPECIMENS STUDIED: Holotype, INPA PLH 326; 45 paratypes, INPA PLH 327, USNPC 86169, 86170, 86171, 86172, 86173, HWML 38762.

DESCRIPTION: Body 272 (219–337; $n = 21$) long, cephalic region directed ventrally; greatest body width 87 (62–110; $n = 21$) usually in anterior trunk. Tegument smooth or with scaled annulations over posterior trunk, peduncle. Cephalic lobes moderately developed. Eyes absent or small, comprised of few granules; posterior pair larger than anterior pair; accessory granules few or absent in cephalic, anterior trunk regions. Pharynx spherical, 14 (12–16; $n = 22$) in diameter. Peduncle broad; haptor 66 (54–75; $n = 23$) long, 92 (78–112; $n = 22$) wide. Ventral anchor 45 (37–50; $n = 20$) long, with well-developed roots, elongate curved shaft, short point; base 15 (13–17; $n = 18$) wide. Dorsal anchor 36 (30–41; $n = 19$) long, with well-developed roots, curved shaft, moderately long point; base 12–13 ($n = 5$) wide. Ventral bar 34 (31–36; $n = 21$) long, broadly U-shaped, with small terminal enlargements; dorsal bar 31 (28–34; $n = 20$) long, broadly V-shaped, with slightly enlarged ends. Hook pair 1—22 (21–24; $n = 3$), pair 2—26 (21–29; $n = 12$), pairs 3, 4—31 (26–33; $n = 39$), pair 5—14 (12–15; $n = 18$), pair 6—20 (17–22; $n = 9$), pair 7—36 (31–40; $n = 15$) long. Copulatory organ 23 (22–24; $n = 14$) long, arcuate; base with small proximal flap. Accessory piece 21 (20–22; $n = 14$) long; distal rod delicate, with elongate terminal hook, subterminal flabellate thumb, small stalked umbell.

Testis 48 (34–67; n = 3) long, 20 (19–21; n = 3) wide, subovate; seminal vesicle prominent. Germarium 47 (26–68; n = 16) long, 17 (12–21; n = 16) wide, irregular; oviduct, ootype, uterus not observed; vitellaria throughout trunk except absent in regions of reproductive organs.

REMARKS: *Enallothecium variabilum* resembles *E. aegidatum* by general morphology of the anchors. It differs from *E. aegidatum* by possessing a more delicate distal rod of the accessory piece and a ventral anchor with a more elongate shaft. The specific name is from Latin (*variabilis* ["variable"]).

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